

THE RELATION BETWEEN FORCE AND VELOCITY IN HUMAN MUSCLE

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Light weights can be lifted more quickly than heavy ones. As the size of the weight is increased the speed of lifting becomes less and less, until eventually no movement takes place at all. As commonly observed, this phenomenon depends partly on the inertia of the object lifted, mainly on the inherent properties of muscle.

Isolated muscle exhibits the same behaviour when it is stimulated: the smaller the opposing force, the more quickly it shortens. Conversely, when allowed to shorten at a predetermined speed, for example in a Levin-Wyman ergometer, the force it exerts diminishes as the speed of shortening is increased. The maximal force is developed when the speed of shortening is zero, that is, when the contraction is isometric. Hill (1922) suggested that stimulation always brought about development of this maximal force, but that during shortening some of the force was used up in overcoming the viscous resistance of the muscle substance. Many experimental results were explained satisfactorily on this basis: for example, those obtained on the inertia flywheel (Hill, 1922; Lupton, 1922), and on the constant speed ergometer (Levin & Wyman, 1927).

In isotonic contractions the relationship between force applied and velocity of shortening was first investigated by Fenn & Marsh (1935). On the viscosity hypothesis the curve relating these two variables should be a straight line; yet they found in isolated muscles both of the frog and of the cat that it was clearly concave towards the origin (Fig. 2). They fitted an exponential equation to this curve (see p. 255).

A later investigation into the heat production during isotonic contraction (Hill, 1938) showed that the shape of the force-velocity curve was governed by the way in which energy was released during shortening: from thermal measurements Hill derived a simple equation relating the two variables

$$(P + a)(V + b) = \text{constant} = (P_0 + a)b,$$

where P = force of contraction, V = velocity of shortening, a and b are constants,

and P_0 is the force exerted at zero speed, i.e. in an isometric contraction. He called this the characteristic equation, and it fitted the mechanical data of Fenn & Marsh, as well as the subsequent results of Katz (1939).

The importance of the force-velocity relationship is twofold. Its close connexion with the pattern of heat production is of theoretical significance; it is of practical interest also, since this relationship determines the mechanical behaviour of muscles loaded in different ways. Once the force-velocity characteristic is established, the variation of velocity in contractions against combinations of forces, inertias and elasticities can be predicted by ordinary mechanics.

For these reasons it seemed worthwhile to investigate the force-velocity relationship in the intact human subject, as suggested by Hill (1940) when he reviewed the inertia-wheel results of Lupton (1922) and found them compatible with a curved force-velocity relationship similar to that in frog's muscle. The first direct investigation of the problem was made by Dern, Levene & Blair (1947), whose results are discussed below (p. 276).

The choice of a movement. Very few movements lend themselves to quantitative study. To be suitable a movement should satisfy the following criteria:

- (1) The joint should be geometrically simple.
- (2) The movement should involve few muscles, which should have small origins and insertions.
- (3) The movement should not disturb rigid fixation of the rest of the body, and should lend itself to graphic registration.
- (4) The movement should be accurately reproducible. This is easiest to achieve if only slight skill is involved.

All these criteria are substantially satisfied by the movement of flexion of the elbow, made with the upper arm abducted at right angles to the body, and in a line with the shoulders; the forearm supinated and moving in a vertical plane. In every instance the movement was made with as much speed and force as the subject could muster. In the inertia wheel experiments mentioned above the same movement was used.

Maximal movements can be repeated with surprising consistency; this is dealt with in detail later. Consistency is maintained, not only throughout a single experiment, but over a period of many months.

Interpretation of results obtained on movements of the whole forearm in terms of the properties of the five flexor muscles is attended by two major difficulties, which are (a) geometrical and (b) nervous.

(a) The origins and insertions of the five muscles are not arranged in any simple way relative to the long axes of the fore- and upper-arms. Consequently, the relationship between the tension in a given muscle, and the torque which that muscle produces on the forearm as a whole, is a complicated function of the angle of flexion, and this function is different for each of the five muscles.

However, as is shown later, only a small error is introduced by assuming that the five muscles are all horizontal when the arm is held in the experimental position. This being so, the horizontal components of the forces and velocities measured at the hand will be proportional to the actual forces and velocities of contraction of the muscles themselves. The experiments relating force to velocity have been made with this picture in mind. The forces and velocities which have been measured are all horizontal components measured at the hand.

(b) It seems to be agreed that even in the most violent effort not all the muscle fibres are fully active at once; but it is not known whether the amount of excitation is constant in such a maximal movement, or whether it depends, on the position of the limb, for example, or the force against which the movement is made. ('Excitation' is meant to express both the number of muscle fibres involved and the frequency of discharge in them.) There is at present no method for determining the degree of excitation in an intact human subject: no satisfactory basis has been demonstrated for the exact quantitative interpretation of electromyograms. All the experiments described in this paper support the hypothesis that the muscles in the body follow a fixed force-velocity relationship in contractions against different types of load, a result which can be accounted for in either of two ways:

(1) That the degree of excitation is constant, and that the muscles themselves follow a fixed force-velocity relationship.

(2) That the degree of excitation varies with the force, but in such a way that for each value of the force, no matter how other conditions alter, only one value of the velocity is possible. This would make the force-velocity characteristic as much a property of the central nervous system as of the muscles.

There is no objective way of distinguishing between these alternatives, but the first seems more probable, for all the studies on isolated muscles indicate that they themselves follow fixed force-velocity relationships.

SECTION I. EXPERIMENTAL DETERMINATION OF THE RELATION BETWEEN FORCE AND VELOCITY IN HUMAN MOVEMENT

In this group of experiments the subject pulled against different weights and the velocity of his hand was measured at the end of each movement.

METHODS

The apparatus (Fig. 1) consisted of a triangular oak lever whose axle ran freely in self-centring ball bearings, which were mounted on blocks at the end of a table. The subject pulled on this lever through a Bowden wire cable in which the tension was varied by varying the suspended weight. The handle attached to the cable was free to rotate about a horizontal axis. The dimensions of the lever were: total length, 39.5 cm.; length of short arm, 7.4 cm.; moment of inertia, 95800 g.cm.².

The subject kept his upper arm fixed during each movement by pressing it up against a padded block of wood screwed to the table. Movement of his body was prevented by a vertical board at the end of the table. In order that the force applied to the arm shall be constant throughout each

movement the cable must remain horizontal. From Fig. 1 it is clear that this will happen automatically provided that the length of lever used is the same as the radius of rotation of the forearm and that its axle is the same height above the table as the centre of rotation of the elbow.

The radius of rotation of the forearm is easily measured by having the subject grasp a pencil while his forearm is swept passively over a sheet of paper. Some care is needed to prevent movement of his upper arm during the process. The circle drawn is remarkably perfect, the variation in radius being less than 1% for a movement of more than 90°. The height of the centre of rotation of the elbow is then the difference between the radius of rotation and the height of the handgrip above the table when the forearm is vertical.

The velocity of each movement was estimated from the charge accumulated on a condenser. As the lever rotated it swept a light spring over the surface of an ebonite sheet, making contact for a brief interval with a recessed brass strip. Contact was made and broken sharply, so the velocity

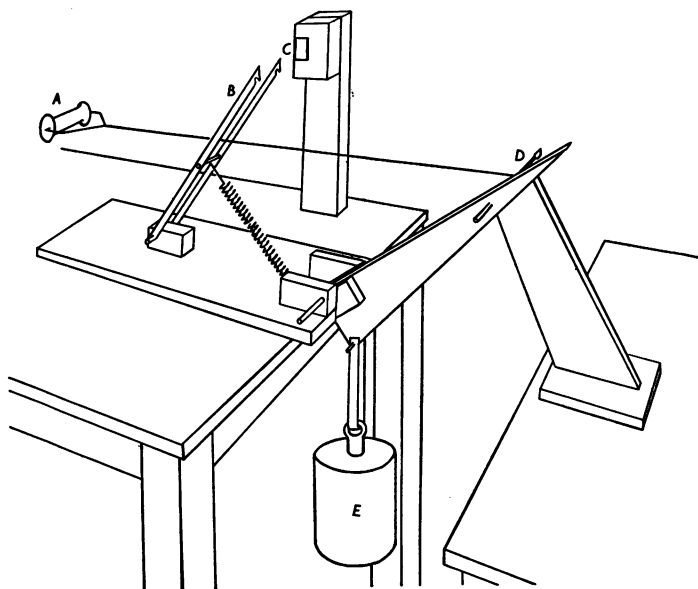


Fig. 1. Isotonic lever for human subjects. *A*, handgrip attached to cable; *B*, catch to hold lever up at the end of movement; *C*, fixed contact; *D*, lever with moving contact; *E*, weight.

of movement could be calculated from the duration of the contact. As soon as contact was closed a condenser began to charge through a resistance. The total charge, Q , which it accumulates, is related to the duration of contact, t , by the expression

$$t = RC \log_e \frac{Q_0}{Q_0 - Q},$$

where R = resistance in ohms, C = capacity in farads and Q_0 = charge when t is very long. Q and Q_0 were measured by discharging the condenser through a ballistic galvanometer. In practice it was found convenient to include a second key in the circuit, in order to discharge the condenser without passing current through the galvanometer; for even with well-insulated circuits (leakage resistance 1000 MΩ.) enough charge leaked across the open contacts to require removal before each determination.

Range of movement. (All angles are measured on the proximal side of the forearm, i.e. full extension is 180°.) The load was supported by a stop so that the lever was at 140° with the horizontal before each movement. At the end of the movement (75°) the load was held up by a spring catch.

The fixed contact was arranged to measure the velocity when the arm was at an angle of 80° with the horizontal. Subsequent experiments have shown that maximal effort does not cease until the arm reaches 70° ; nor is there appreciable evidence of antagonist activity before this point.

Measurement of isometric tension. P_0 , the isometric tension, appears in the characteristic equation. It was measured by a simple spring balance, with the forearm at an angle of 80° with the horizontal, i.e. in the position at which the velocity was measured.

Procedure. Preliminary experiments on two subjects showed that satisfactorily consistent results were obtained and these yielded a curve of force against velocity similar in shape to those found by Fenn & Marsh (1935), Hill (1938) and Katz (1939) on isolated muscles. A large-scale experiment was therefore carried out to determine more precisely the relationship between force and velocity in one subject.

Units. All forces are given in megadynes, where 1 megadyne = 10^6 dynes or approximately 1 kg.wt.

Arrangement of experiment. The tension at the hand was varied in eleven steps from 0 to 15.23 megadynes and at each step thirty measurements of the velocity were made, 330 determinations in all. Only five velocity measurements at the same tension were made at any one time and each one followed a rest period of at least a minute; fatigue was thus avoided. The order in which the sixty-six groups of five determinations were made was decided from random number tables and the whole experiment was spread over a period of 2 weeks. This arrangement was adopted in order that each group of measurements should represent a true random sample from the population of such measurements, to which sampling theory might be legitimately applied.

RESULTS

The thirty velocity measurements made at each tension were in every case distributed normally about their mean value. Even in the worst distribution the shape constants $\sqrt{b_1}$ and a , which measure skewness and flatness respectively (Geary & Pearson, 1938), were within normal limits:

$$\begin{aligned}\sqrt{b_1} &= 0.08 & P &\gg 0.05, \\ a &= 0.862 & 0.10 &> P > 0.05.\end{aligned}$$

The experimental curve of mean velocity against tension is plotted in Fig. 2. As the experimental relationship between force and velocity was now established with known precision, it remained to be seen whether this could be described by the characteristic equation. Since that can be written

$$\left(\frac{P}{a} + 1\right) \left(\frac{V}{b} + 1\right) = \frac{P_0}{a} + 1,$$

the shape of the characteristic curve is fully defined by the ratio a/P_0 .

After a few trials with different values of a/P_0 , it became clear that the experimental results were *not* fitted by the characteristic equation, except at tensions greater than about $0.3 P_0$. However, the experimental results as they stand are not engendered by the muscles alone; they result partly from the properties of the apparatus. It seemed likely that the inertia of the apparatus and forearm might so diminish acceleration that the full velocity could not be reached before the movement was completed. This effect would naturally be greatest when the final velocity was greatest, and might account for the observed departure from the characteristic equation. The forearm provides most of the inertia when only small weights are lifted, so there is little point in improving

the apparatus. Instead, allowance is made mathematically for the effect of inertia.

Correction for inertia of apparatus and arm. Imagine that the contractile part of the muscle is pulling against the inertia of a mass M as well as a constant force F . The force which the muscle can exert at any point is some function, as yet unknown, of its velocity of shortening at that point; let us say $P=f(V)$. But, in the case considered,

$$P = F + M \frac{dV}{dt}, \quad \text{so} \quad f(V) = F + M \frac{dV}{dt}.$$

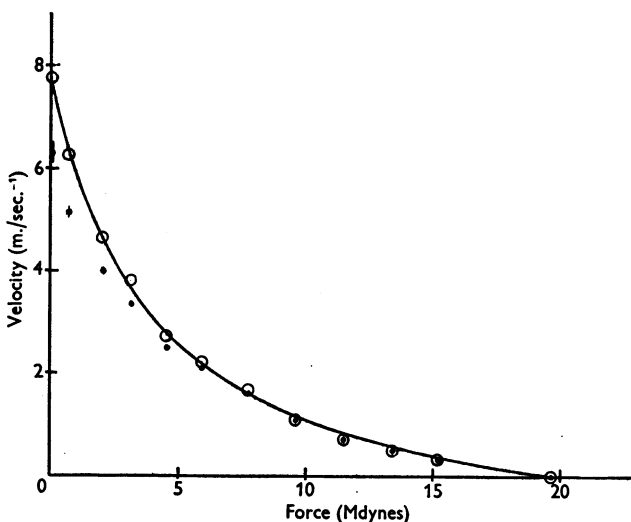


Fig. 2. Experimental relation between force and velocity (subject D.W.). Dots: means of thirty determinations of velocity. Six times the standard error is plotted as a vertical bar through the mean. At many points it is too small to be visible on reproduction. Circles: experimental points after correction for inertia. Curve drawn from $(P \times a)(V \times b) = (P_0 \times a)b$ with $a/P_0 = 0.20$.

The solution of this equation will describe how the velocity of the system rises during the movement, thus making it possible to decide whether inertia does limit acceleration in the way suggested. The immediate problem was to discover whether the characteristic equation represents the true force-velocity relationship in the muscle and this was done by substituting

$$P = \frac{(P_0 + a)b}{V + b} - a \quad \text{for} \quad P = f(V)$$

in the above equation. Then

$$\frac{(P_0 + a)b}{V + b} - a - F = M \frac{dV}{dt}. \quad (1)$$

The theoretical effect on acceleration was then compared with the effect observed experimentally.

The method for finding the correct values of a and b is somewhat involved, as they should be based on the $P:V$ curve *after* correction for inertia. In Appendix A an expression is derived for the amount by which the actual velocity at the end of the movement falls short, owing to inertia, of the theoretical final velocity. It involves F and P_0 , which are already known; M , which, as shown below, can be measured; x , the measured length of pull and the constants a and b , which it is required to find. The true values of a and b can then be calculated from the experimental $P:V$ curve in the following way:

(1) Provisional values of a and b are estimated by fitting a curve directly to the experimental data.

(2) With these and the known values of F , P_0 and M the velocity deficit is calculated for each experimental point. When each deficit is added to its experimental point a new set of points above the first is obtained.

(3) Fitting a new characteristic equation to this set of points yields new values of a and b , with which the whole cycle is repeated.

(4) After three or four repetitions there remains no discrepancy between the corrected points and the characteristic equation from which they are derived. These final values of a and b are therefore the correct ones.

The magnitude of the correction involved can be seen from Figs. 2 and 3, where corrected experimental points are plotted with their appropriate theoretical curve. It is clear that the characteristic equation gives a good description of the corrected experimental results. Of course, other equations may do just as well; for example, that derived by Fenn (1938)

$$P = P_0 e^{-aV} - kV,$$

in which a and k are constants. It is the shape of the curve which is important, while the equation used to describe that shape is largely a matter of convenience.

The experiment was not done in such detail on the other four subjects, and each point is based on five instead of thirty determinations of velocity. Each was corrected for inertia in the way described above. Their fit with the characteristic equation is in every case quite good, and the range of values of a/P_0 is approximately the same as that reported by Katz (1939) in the frog. It is also interesting to note that, although the maximal force exerted varies from 12 to 20.5 megadynes, the maximal velocity attained is relatively constant, a finding reported previously by Dern *et al.* (1947). This result might have been anticipated on dimensional grounds. Animals of different size, but similar shape, greyhounds and race-horses for example, have the same maximal running speed.

The results on the five subjects are collected in Table 1.

Determination of inertia. The inertia M whose value was used in the previous calculation consists of three parts, all of which should be expressed in terms of their equivalent mass at the hand.

(1) The equivalent mass of the weights is found by multiplying their mass by $(S/L)^2$, where S and L are the short and long arms of the lever.

(2) The moment of inertia of the lever itself is most easily found by measuring the moment m which it exerts when horizontal, and also its natural period of oscillation T . Then, moment of inertia $I = 4\pi^2 T^2 m$, and equivalent mass $= I/L^2$.

(3) The moment of inertia of the forearm can be determined in several ways. Braune & Fischer (1894) suspended the limbs of cadavers on steel pins and measured their moment and period. The same principle was used by Hill (1940), with his own completely relaxed forearm. Fenn (1938) measured the initial

TABLE 1. Force-velocity characteristics of five subjects

	Subject	Age	Sex	P_0	V_0	$a/P_0 = b/V_0$
1	J.H.	22	F.	12.0	670	0.33
2	L.M.	24	M.	20.0	700	0.48
3	R.S.	20	F.	12.0	650	0.42
4	M.R.	22	M.	20.5	600	0.37
5	D.W.	23	M.	19.6	775	0.20

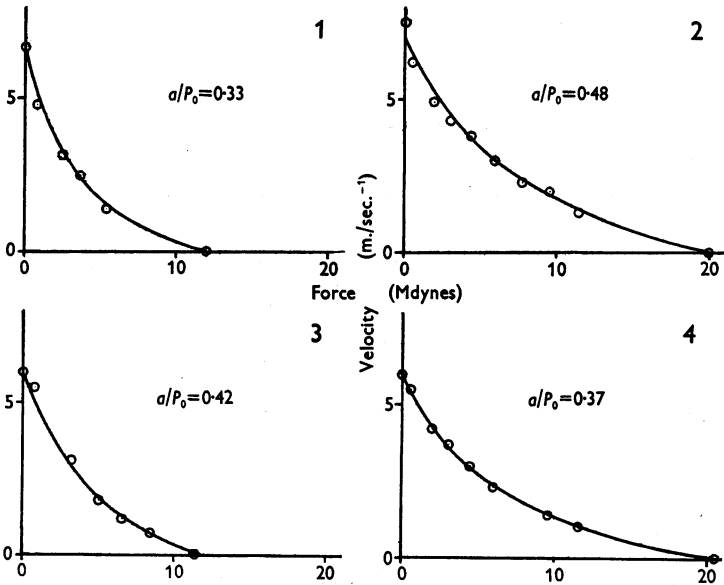


Fig. 3. Force-velocity characteristics of four subjects. Circles: experimental points corrected for inertia. Curve drawn from the characteristic equation.

acceleration following sudden application of a known force, and his results were of the same order of size as those of Braune & Fischer, that is, about 0.5 kg.cm.².

In the present experiments a direct method was used. The forearm, with the fist held in the experimental position, was lowered by 2 cm. steps into a tall jar of tepid water. Each segment of the arm displaced its own volume of water over into a beaker, where it was weighed. The best device for collecting all the displaced water was found to be an open-ended siphon with its outlet a few inches below the rim of the jar; care was required to avoid breaking the siphon by even a slight withdrawal of the arm. This arrangement was very sensitive

and reliable: when 10 c.c. of water was added with pipette to the jar, this volume was always recovered to within 0.2 c.c. from the beaker.

The total volume of each 2 cm. segment of forearm being known, the proportion of bone was found by repeating the procedure with a skeleton chosen to match exactly the radiograph of the subject's arm. The mass of each segment was then calculated on the assumption that the density of soft tissues was 1 g./c.c.; while that of the bones was found to be 1.4 g./c.c. after repeated heating and cooling under water had removed air bubbles. Then the moment of inertia $= \sum M_n r_n^2$, where M_n is the mass of the n th segment, distant r_n from the joint axis.

Since all forearms are of similar shape the inertia was not determined directly on the other four subjects, but was calculated from that of subject D.W., multiplying by $\left(\frac{\text{length of forearm of subject}}{\text{length of forearm of subject D.W.}} \right)^5$.

For subject D.W., moment of inertia $= 0.53 \text{ kg.cm.}^2$, equivalent mass at 32 cm. $= 0.52 \text{ kg.}$, maximum moment $= 21.9 \text{ megadyne.cm.}$

The variation of equivalent mass with position. From the point of view of the flexor muscles the equivalent mass of the forearm is not the same in all positions of the limb. The equivalent mass of the forearm is only equal to (moment of inertia)/ r^2 when the angle of flexion is 90° . At any other angle θ the equivalent mass is greater by the factor $1/\sin^2\theta$. The variation is small (13%) between 70° and 110° , but increases steeply outside these limits, so that at 50° and 130° the discrepancy has reached 69%. Fortunately, in the slower movements where the early part of contraction is of particular interest, only a small part of the total inertia is provided by the arm; the equivalent mass of the weights does not vary with the position of the limb.

SECTION II. THE RISE OF VELOCITY IN ISOTONIC CONTRACTIONS

The method of correcting for inertia used in the previous section is based on the assumption that one can predict mathematically how the velocity will rise in a single contraction. The only property attributed to the muscle and its central nervous connexions was that at any instant its velocity of shortening should be some definite function of the tension which it exerted. It was shown that the characteristic equation gave a good approximation to this function.

However, it remained to be seen whether the velocity did rise in the way predicted; which involved measurement of the velocity throughout the movement and not just at one point as in the previous experiments.

METHODS

Three different methods were used to register the variation in velocity during single contractions.

The first method used was very simple and quickly set up. A small electromagnet attached to the lever was energized by current from the mains. In this way a small pointer was caused to vibrate at 100 c.p.s. in a direction parallel with the long axis of the lever. As the subject pulled,

the pointer drew out the arc of a circle on a piece of smoked glass held vertically in a Palmer stand. On this arc were superimposed undulations 10 msec. apart. After varnishing the record the distance was measured between each undulation and the starting position. The increment in displacement is clearly proportional to the average velocity during that period.

In the second method used, high-speed cine-films of the movement were taken, and the horizontal movement of the hand between frames measured. A clock and a scale of decimetres were included in the picture to provide an absolute calibration in terms of velocity.

Both methods suffer from two defects. The distances to be measured are small, so slight inaccuracy causes marked scatter of the points representing velocity: also both are time-consuming, reducing the number of experiments performed. A more elaborate and accurate apparatus was therefore devised.

A small coil of 100 turns was mounted on the axle of the lever as shown in Fig. 4 so that it rotated in the gap between the poles of a powerful magnet. The voltage induced depended on the speed of rotation of the coil.

The magnetic flux linked with coil is

$$N = HAn \sin \theta,$$

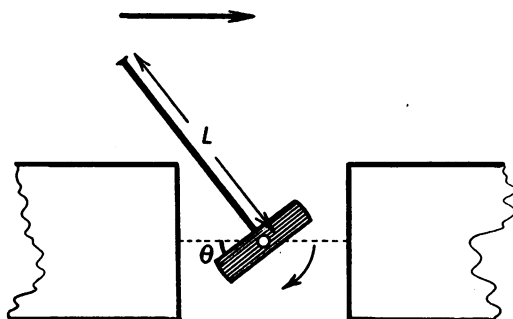


Fig. 4. For explanation see text.

where H = magnetic field, A = area of coil, n = number of turns and θ = angle between axis of coil and the magnetic axis; for the voltage developed is

$$E = -\frac{dN}{dt} = -HAn \cos \theta \frac{d\theta}{dt},$$

and the horizontal component of velocity of hand is $V = L \cos \theta \frac{d\theta}{dt}$, where L = length of lever. Therefore

$$E = -\frac{HAn}{L} \times V.$$

That is, a voltage is developed which is proportional to the horizontal component of the velocity of the hand.

In order to test for non-uniformity in the magnetic field, the coil was detached from the lever and rotated at constant speed by a small electric motor. The alternating voltage developed was amplified and applied to a Wien bridge adjusted to remove the fundamental frequency. The residue of harmonic had 1% of the original amplitude.

To register the velocity of the hand, current from the coil was passed to a Downing galvanometer (period 12 msec., sensitivity 1.66×10^{-7} amp./mm. at 1 m., resistance 50 Ω .), whose deflexion was recorded on a falling-plate camera. It was arranged that the galvanometer should be always critically damped, and a series resistance of 100–1000 Ω . was included to limit the current drawn from the coil. Time marks were provided every 20 msec. by a stroboscopic lamp.

At one point the absolute velocity was measured by the condenser method already described, to provide a calibration on each record. This point was identified on the trace by a bright flash from

the stroboscopic lamp, which was triggered from the condenser circuit, but did not withdraw any current from it.

In later experiments the velocity-time curve was displayed on a long after-glow cathode-ray tube, using a single-stroke time-base and a d.c.-connected Y amplifier with a gain of about 3000. This is by far the best experimental arrangement.

RESULTS

The subjects pulled with maximal effort against a succession of weights in exactly the same way as before. A typical set of velocity-time curves is shown in Fig. 5A.

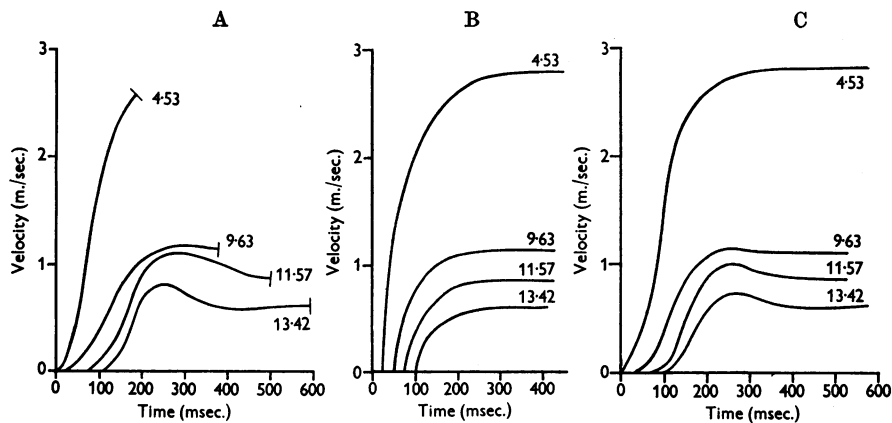


Fig. 5. Velocity-time curves. Subject D.W. A, Experimental curves. The bar at end of each curve marks the point at which lever hits catch, just after its velocity has been measured for calibration. Subsequent rapid and irregular fall in velocity not shown. B, Theoretical curves. Calculated from $(P_0 + a)b/(V + b) - a = F + M dV/dt$ (see Appendix A). C, Theoretical curves. Calculated electrically from equation 2, p. 261. Figures on graphs indicate tension (megadynes) against which pull was made.

The theoretical curves, derived from

$$\frac{(P_0 + a)b}{V + b} - a = F + M \frac{dV}{dt},$$

are shown in Fig. 5B. The integrated form of the equation, from which the points are actually calculated, is given in Appendix A.

As expected, when the tension is small, e.g. $F = 4.53$ megadynes, there is not time enough to reach a steady velocity before the movement is brought to a stop. This illustrates the importance of the inertia correction used in section I. However, it is clear that although each theoretical curve does rise to the right final velocity, the *mode of rise* is rather different from that found experimentally:

(1) The calculated curves rise sharply from the base-line. Experimentally each begins more gently, with a distinct concavity upwards. The reason for this concavity was thought to be that all the motor units did not become active at once. Fenn (1938) suggests that excitation takes about 40 msec. to reach its

maximum, and this agrees quite well with the duration of the concavity. An alternative explanation is given below.

(2) Experimentally, when the force is large, e.g. $F=11.57$ megadynes, the velocity is seen to rise to a peak before settling towards its steady level. When the force is larger still, e.g. 13.42 megadynes, the velocity executes a damped oscillation about its final value. These observations have been repeated consistently in ten subjects. To explain them, three possibilities were considered.

(1) *Flexion of the wrist might occur suddenly, early in the movement.* The extra shortening represented by the peak of the velocity-time curve is equal to $\int V dt$, that is, the area of the peak. This is only about 4 cm. with even the greatest peaks, so, if it occurred quickly enough, flexion of the wrist could account for the observed result.

The question was investigated by photographing the movements with a high-speed camera, kindly made available by Messrs Kodak. The films showed that there was some flexion of the wrist early in the movement, but that most of it took place after the velocity peak was over. Moreover, the shape of the velocity-time curve was not altered when the wrist was held in full flexion throughout the movement by a light plaster-and-metal splint.

(2) *The degree of excitation might vary during the movement.* If the degree of excitation to a muscle alters, its isometric tension, P_0 , will be changed. Now in the characteristic equation P_0 appears as a constant. If, therefore, it is shown that the same equation applies at every instant during a contraction, P_0 must remain constant and there can be no variation in the degree of excitation.

Direct investigation of nervous activity was therefore postponed until it had been decided whether or not the characteristic equation did apply throughout the movement. That it did became clear on considering the third possibility.

(3) *Oscillation might result from the presence of an inert elastic element between the contractile part of the muscle and its load.* The presence of such an element in isolated muscle was first demonstrated by Levin & Wyman (1927). Hill (1938) showed that a dual structure consisting of 'characteristic' elements in series with inert elastic ones could also explain the effects which they attributed to visco-elasticity.

Measurements of heat production also supported the hypothesis. The amount of mechanical energy supposedly stored in the elastic element at the peak of contraction could be calculated: it was found to be of the same order of size as the measured heat of relaxation. The heat was therefore considered to be merely degraded mechanical energy. More recently it has been shown (Hill, 1949) that when the conditions of shortening are arranged so that no mechanical energy is stored, no relaxation heat is found.

In human experiments the presence of such an element was suggested by the observation that peaking and oscillation in the velocity-time curve was

increased when a spring was incorporated in the cable. The mechanical system visualized was that shown in Fig. 6. During the initial acceleration energy is stored in the elastic element, to be released again as the velocity approaches its steady value. The way in which the velocity of such a system should rise can be predicted by simple dynamics. The point to be tested is whether prediction is similar to experimental fact. In Fig. 6: F =isotonic force, P =tension in muscle, v =velocity actually measured, V =velocity of shortening of muscle, G =compliance (strain/stress) of elastic element:

Equating forces, $P = F + M \frac{dv}{dt}$. Equating velocities, $V = v + G \frac{dP}{dt}$. But $V = \frac{(P_0 + a)b}{P + a} - b$, from the characteristic equation. Combining these equations to eliminate P and V

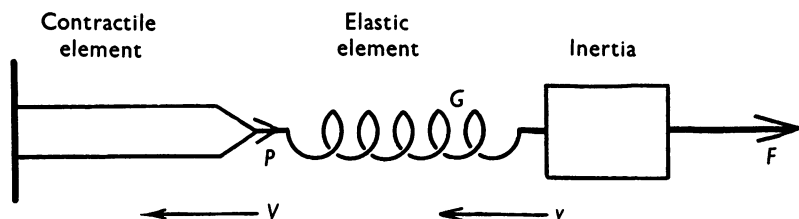
$$v + GM \frac{d^2v}{dt^2} = \frac{(P_0 + a)b}{F + M(dv/dt) + a} - b. \quad (2)$$


Fig. 6. Proposed structure of muscle pulling against a load.

This non-linear differential equation cannot be integrated; that is, it is not possible to obtain from it an expression without differentials giving v in terms of T . A numerical solution must be obtained in each individual case by arithmetical integration.

Two examples worked out in this way looked similar to experimental curves, but in order to test the theory fully it was obviously necessary to compare calculated and experimental results under a variety of conditions.

In practice there was an obstacle to carrying out this plan: arithmetical integration is an excessively laborious and time-consuming process. An electrical method for performing the calculations, described elsewhere (Wilkie, 1950) was therefore developed.

Of the parameters of the equation; F , P_0 , M , a and b are all known from section I, while an independent method of calculating G from measurements of isometric tension will be described below. (Section III.)

The variation of compliance with tension has not been taken into account, the central value at $0.67 P_0$ being used (Table 2). That this makes little difference to the shape of the velocity-time curve was shown by arithmetical

solutions using linear and non-linear compliances. The result would be expected, since the tension varies only slightly in each isotonic contraction.

The experimental (*A*), and calculated (*C*), curves are shown in Fig. 5. The similarity between the shapes of the two sets of curves supports the hypothesis that there is an inert series elastic element between the contractile part of the muscle and its load, and that the characteristic equation is obeyed throughout the movement.

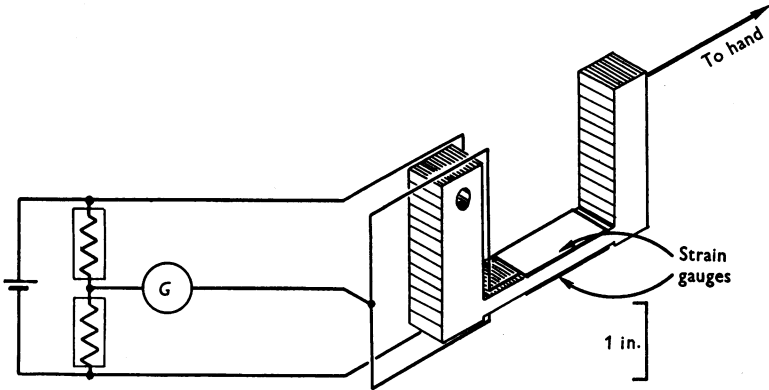


Fig. 7. Arrangement of resistance strain gauges and associated circuit for measurement of isometric tension.

The initial concavity is accounted for as well as the peaking, so that it is unnecessary to suppose that the maximal excitation develops only slowly. Indeed, the characteristic equation is obeyed so well throughout the movement that there cannot be any large variation in the degree of excitation.

The inertia correction used in section I is barely affected by these new findings, for it is only applied when the tension is small and 'peaking' is not evident. With large tensions the peak has disappeared long before the velocity is measured.

SECTION III. THE RISE OF TENSION IN ISOMETRIC CONTRACTIONS

The force developed in an isometric contraction requires an appreciable time to reach its final value.

In order to explain the slow rise in tension, Hill (1938) made the assumption that muscle is a two-component system consisting of actively contractile and passively elastic structures in series. During isometric contraction the active elements were imagined to shorten at the expense of the passive ones, the total length of muscle remaining constant. His conclusions were confirmed experimentally by Katz (1939).

Apart from their intrinsic interest, isometric experiments are important in

providing an independent means for estimating the series compliance, G , of the elastic element.

If one assumes that the relationship between force and velocity in the contractile elements is the same under isometric as it was under isotonic conditions, the compliance of the series element can be calculated from the rate of rise of isometric tension.

Let tension exerted by muscle = P , series compliance = G . Then, rate of shortening of active element is

$$V = \frac{(P_0 + a)b}{P_0 + a} - b.$$

Rate of lengthening of passive element = GdP/dt . Equating these

$$G = \frac{(P_0 + a)b}{P + a} - b \left/ \frac{dP}{dt} \right.$$

The constants in this equation are all known from section I: values of P and dP/dt were obtained from experimental tension-time curves.

METHOD

In preliminary experiments the isotonic lever was replaced by a stout bracket of spring steel, bolted down to the table. The cable and handle were attached to its free end and the deflexion of the bar magnified by an arrangement of mirrors giving a light path of 3 m. Records of the displacement were made by a falling-plate camera.

Such apparatus is easily set up, and has a suitably short period of vibration (31 msec. in this case), but it is difficult to mount the spring so rigidly as to prevent relative movement between it, the optical system and the camera.

A far more convenient and adaptable tension-measuring device was built with resistance strain-gauges, each of which contains a grid of fine wire whose electrical resistance is increased on stretching. A pair of gauges (British Thermostat Company, SE/A/11, 2500 Ω .) were mounted on a piece of mild steel of the shape shown in Fig. 7. They formed two arms of a Wheatstone's bridge, which was completed by a second pair of gauges. The degree of unbalance of the bridge was indicated directly on a Downing galvanometer (period 50 msec., sensitivity 8×10^{-9} amp./mm. at 1 m., resistance 100 Ω .).

The advantage of this paired arrangement of gauges is that temperature effects are neutralized; also the sensitivity to tension is doubled while the response to twisting is reduced.

The calibration curve, which was a straight line, was based on six measurements at each of twenty-two different tensions. The average standard deviation within the groups of six was only 0.58% of the half-scale deflexion.

The tension gauge was mounted on the isotonic lever, which was held vertical by a rigid strut. The subject pulled from the far end of the table, exactly as in the previous experiments.

RESULTS

The relationship between isometric tension and time in subject D.W. is shown in Fig. 8A, curve a , which is the mean of five independent observations. From this figure the value of dP/dt was found at chosen intervals of P , by drawing the geometrical tangent to the curve. Knowing dP/dt and P at a number of different points on the curve, the compliance at these points was calculated from the equation above.

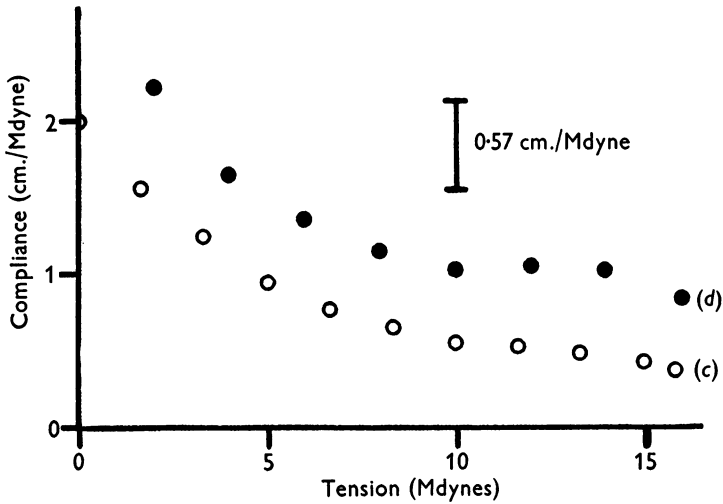
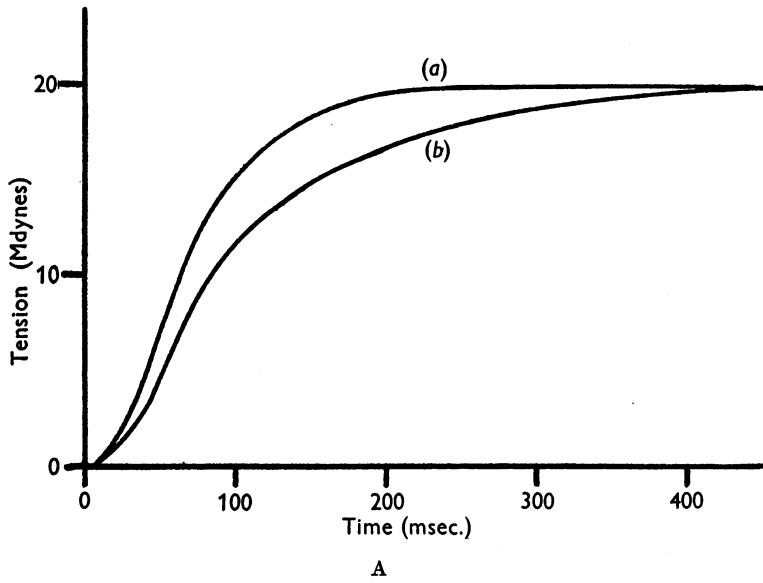


Fig. 8. A, The rise of isometric tension with time. Subject D.W. (a) arm alone; (b) with compliance of 0.57 cm./megadyne added to cable. B, The variation of compliance with tension; calculated from curves of A. (c) arm alone; (d) compliance of 0.57 cm./megadyne added to cable. Note the approximately constant vertical displacement between the curves.

The result of this calculation is shown in Fig. 8B, curve *c*, where it is seen that the compliance diminishes as the tension increases. This behaviour is similar to that of resting muscle; or of a fibrous structure, a knitted stocking for example, whose fibres do not all run in the same direction or do not all start tight.

However, if the maximal excitation takes an appreciable time to become established, the resulting slow rise in tension will also appear as an increased compliance when the tension is low, indistinguishable from a true increase in compliance. In order to provide independent evidence on this point the experiment was repeated with a spring (compliance 0.57 cm./megadyne) in series with the cable.

The effect of added compliance. The new tension-time curve, *b* in Fig. 8A, rises more slowly than before. From it is calculated the compliance-tension curve *d* in Fig. 8B. This curve is found to be displaced vertically by an amount corresponding approximately to the known added compliance. Now if the curvature of Fig. 8C were due to the slow increase of excitation, this curvature should be diminished by increasing the series elasticity; for a given tension would then be reached later in the contraction, after the

TABLE 2. The series compliance measured at the hand. Values correspond to a tension of $0.67 P_0$

Subject	J.H.	L.M.	R.S.	M.R.	D.W.
Compliance (g.cm./megadyne)	1.1	1.1	0.6	3.6	0.5

excitation had become steady. As in Fig. 8C and D are the same shape, it is likely that this is determined by the muscle compliance. The series compliance was determined in the same way on the other four subjects, and the results are shown in Table 2. The compliance varies with the tension, but only one value is given in the table, corresponding to $P = 0.67 \times P_0$. The effect of adding extra compliance (0.57 cm./megadyne) to the cable as described above, was to produce a displacement of 0.4–0.7 cm./megadyne in the compliance-tension curve.

The values given in Table 2 seem surprisingly large, but it should be remembered that they were calculated as though the compliance were localized at the hand. Variation in length in the muscles is magnified approximately seven times by the lever of the forearm and their force is diminished by the same ratio; so the compliance measured on isolated muscle would be only $(1/7)^2$, or about 2%, of the value shown in the table.

The anatomical site of the elastic element is a matter of speculation. It seems unlikely that all the compliance resides in the tendons, which are relatively rigid structures. Possibly the muscle fibres themselves contain series elastic elements, which one is tempted to identify with the isotropic disks of the myofibrils, for Buchthal & Lindhard (1939) have shown that these become stretched during isometric contraction by active shortening of the anisotropic

disks. However, there is at present no other evidence for this view than superficial resemblance.

By integrating under the compliance-tension curve it is possible to calculate the total lengthening of the elastic element under full isometric tension. In the case of subject D.W., Fig. 8B, allowing for the lever ratio of the forearm, this corresponds to about 10% of the resting length of the muscle. In isolated muscles the ratio is regularly in the same region, from 10 to 15%.

SECTION IV. THE INTERPRETATION OF MOVEMENTS IN TERMS OF MUSCLES

The experiments of the preceding sections have shown that in maximal voluntary movements there is a definite relationship between velocity of movement and force exerted, both being measured horizontally at the hand.

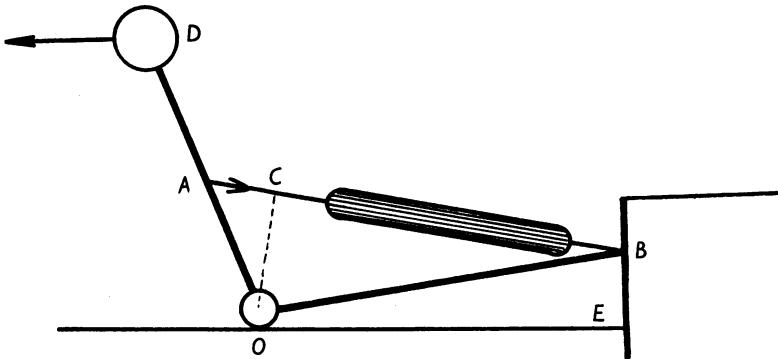


Fig. 9. Diagram of fore- and upper-arms showing the action of a single flexor. *B* and *A*, origin and insertion; *O*, elbow; *D*, hand-grip. Note that the humerus is not horizontal.

This relationship applies at every instant during the shortening, and it can be represented by the characteristic equation. Whether the properties found experimentally on whole movements are also the properties of individual human muscles has already been discussed, and throughout this paper the two have been tacitly identified in order to simplify explanation.

As indicated earlier, it will be necessary to deal with the mechanical and nervous aspects of the problem separately.

The mechanics of the elbow joint

The action of the five flexors of the elbow joint was analysed in considerable detail by Braune & Fischer (1890), who set out to discover what contribution each muscle made to the total torque at the elbow. At 5° intervals of flexion they measured the equivalent lever arm of each muscle, that is, the perpendicular distance from muscle to joint axis. Subsequently, they calculated the equivalent lever arm trigonometrically, using the measured distances of origin and

insertion from the joint axis; this calculation agreed well with their direct measurements.

The agreement is of importance, since a similar calculation is used in this paper to determine the ratio between the tension in each muscle and the horizontal force which that muscle produces at the hand. It has been assumed up to this point that the lever ratio was constant throughout flexion. That this is actually the case is shown below.

Consider one muscle. It is required to calculate OC , the equivalent lever arm (see Fig. 9).

$$\text{Equivalent lever arm} = OC = \frac{OBA \sin AOB}{\sqrt{(OA^2 + OB^2 - 2OAOB \cos AOB)}},$$

and $\text{lever ratio} = \text{horizontal force/tension in muscle} = \frac{OC}{OD \sin AOE}.$

The lever ratio has to be calculated for each muscle over the whole range of shortening used experimentally. This involves measuring AO and OB for each muscle.

TABLE 3. Distances from joint axis in centimetres

Subject	M.R.		D.W.		Braune & Fischer Means of four subjects	
	OA	OB	OA	OB	OA	OB
Pronator teres	13.50	1.70	11.35	1.38	11.35	1.37
Extensor carpi radialis longus	24.00	3.00	25.11	2.90	22.05	3.50
Brachialis	2.70	9.00	3.14	12.40	3.40	9.95
Biceps	4.60	28.50	4.48	32.00	4.50	28.32
Brachio-radialis	24.10	7.00	25.02	7.30	20.92	8.57
Hand-grip	32.0		32.0		—	—
Wristlet	25.4		25.2		—	—

X-ray photographs were taken of the arms of subjects M.R. and D.W., held in the experimental position and with the tube at least 5 ft. from the plate. The origins and insertions of the five flexors were identified from the photographs quite easily by comparing them with a skeleton of nearly the same size. The distances of these points from the joint axis were then measured (Table 3). In both subjects the angle BOE between humerus and horizontal was about 5° . The lever ratio at different angles of flexion was then calculated. The result is shown in Fig. 10.

It is clear that the lever ratio remains practically constant over the range of movement used experimentally, the only departure (radialis longus) being by extensor carpi.

The force-velocity relationship in individual muscles. Some uncertainty remains about the force-velocity relationship in individual muscles, because in each muscle the velocity of shortening is proportional to the horizontal component of the velocity of the hand (by exactly the argument detailed above in the case of forces), while the horizontal force at the hand is the *sum* of a number of proportional components, one from each flexor.

To illustrate the effect of this, imagine that the hand moves with a certain velocity V' . The various flexor muscles shorten at speeds proportional to V' , and the tension which each one exerts is some function, probably the characteristic function, of the speed of shortening.

As V' increases, the rate of shortening of one of the muscles may eventually exceed its maximum unloaded speed V_0 , so it will no longer be able to develop

tension. That is, it will drop out of action while the other flexors are still functioning. This is bound to happen unless in each muscle V_0 is proportional to OA (Fig. 9), the distance from insertion to joint axis. In the intact subject it is not possible to determine V_0 separately on each muscle; but if one assumes that the muscle fibres are similar in all the flexor muscles, V_0 should be proportional to the length of the muscle, P_0 to its cross-section. This assumes, of course, that the fibres all lie parallel with the long axis of the muscle. Examination of cadavers shows that this is in fact the case for all the flexors except brachialis.

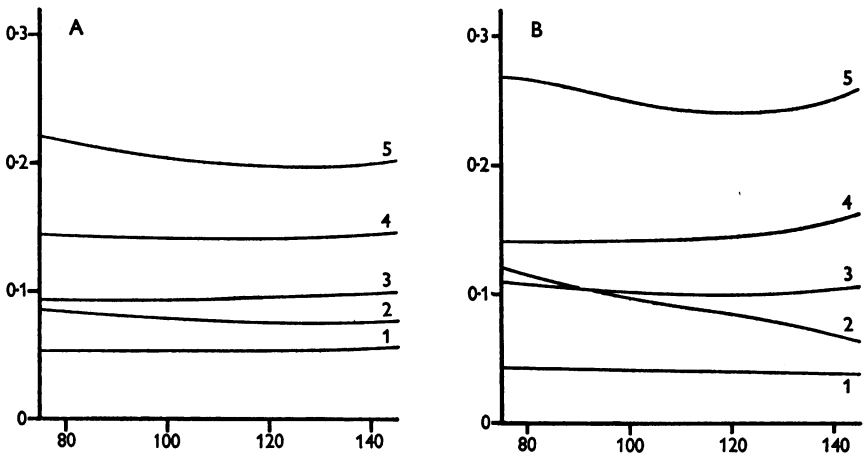


Fig. 10. Lever ratio at different angles of flexion. Abscissa: angle between forearm and horizon.

Full extension is 180° . Ordinate: lever ratio = $\frac{\text{horizontal tension at the hand}}{\text{tension in muscle}}$. Curves: (1) Pro-

nator teres; (2) extensor carpi radialis longus; (3) brachialis; (4) biceps, both heads taken together; (5) brachio-radialis. Graph A. Subject M.R. Graph B. Braune & Fischer (1890); mean value from four subjects.

The ratio (distance from axis OA /length of muscle) is certainly not constant, as it varies from 0.3 (brachialis) to 0.15 (biceps). If one knows the approximate dimensions of each muscle (Braune & Fischer, 1890, p. 291) it is quite a simple matter to calculate in arbitrary units the force developed by each muscle at various velocities of movement of the hand, for a given common value of a/P_0 . The total tension is then the sum of the individual tensions, allowing for the difference in their lever arm. The resulting curve of total tension against velocity, e.g. Fig. 11, has discontinuities at the points at which brachialis and brachio-radialis drop out of action. Nevertheless, it can be fitted quite well by the characteristic equation with $a/P_0 = 0.209$.

The value of a/P_0 for the combined curve is always small compared with that of the individual fibres, and it is difficult to explain how combined curves with a/P_0 as large as 0.48 (subject L.M.) could be built up in this way. It is likely,

therefore, that the intrinsic speed $(-dl/dt)/l$ under zero load, is not the same in the fibres of the different muscles. The same finding was reported in animals by Denny-Brown (1929), who demonstrated large differences between the speed of operation of different muscles in the same animal.

Even although there is some uncertainty about the exact *form* of the force-velocity relationship in the individual muscles, it is practically certain that each of them does follow a fixed force: velocity characteristic; for when the hand

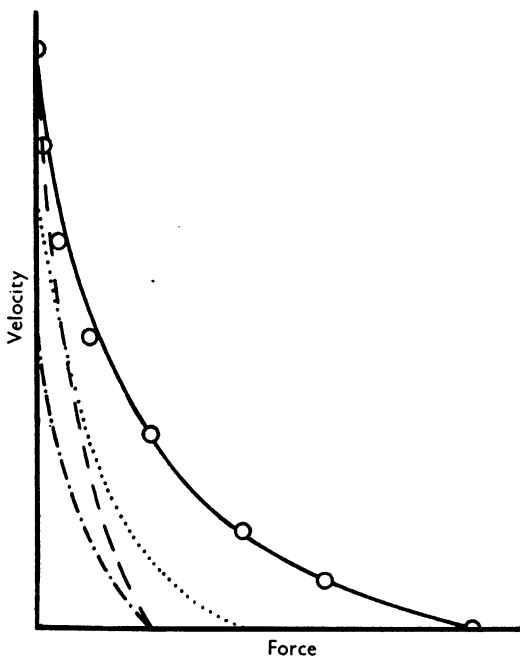


Fig. 11. Force-velocity relation in the three principal flexors of the elbow and in the whole limb. Values calculated on the assumption that the muscles are composed of similar fibres with $a/P_0=0.4$. Forces and velocities expressed in arbitrary units as they would be measured at the hand., brachialis; — — —, biceps; — . — . —, brachio-radialis; ○ — ○ — ○ — whole limb. Curve drawn from characteristic equation with $a/P_0=0.209$.

moves at constant speed, each muscle shortens at constant speed, and the *total* tension remains constant. If the force exerted by each muscle does vary other than with the velocity, this variation must cancel out among the different flexors. It is very unlikely that this accident would be repeated in each of five subjects.

The tension-length diagram of human muscle. The isometric tension which a given muscle can exert varies with its length. The isometric tension, P_0 , appears in the characteristic equation as a constant, so this equation can be expected to apply over only a limited range of shortening.

In order to ensure that this range was not being exceeded in these experiments, the variation of isometric tension in different positions of the limb was investigated.

The P_0 used in the equation is simply the horizontal tension exerted by the hand at zero speed of shortening and it is quite simple to measure this directly. It would be of considerable theoretical interest to discover what is the tension-length relationship in the individual flexor muscles. Unfortunately, the effect of one muscle cannot be isolated from that of the others; however, the number of active muscles can be cut down from five to two by anaesthetizing the radial nerve in the spiral groove. The resulting problem in interpretation is discussed below.

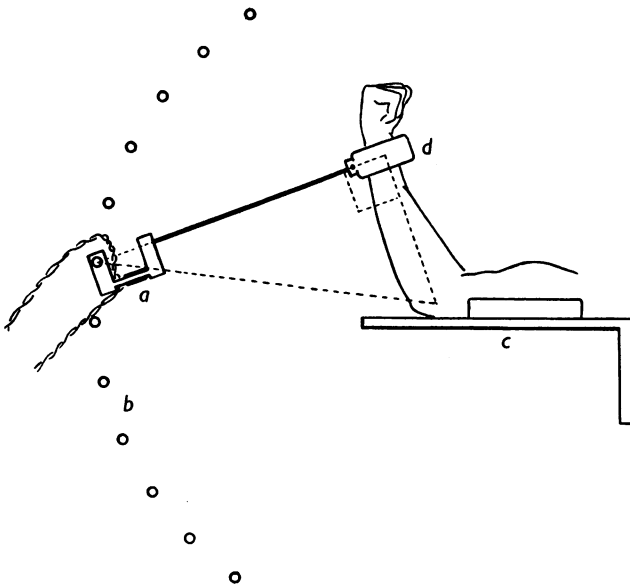


Fig. 12. Apparatus for measuring the isometric torque exerted in flexion of the elbow. *a*, tension gauge; *b*, circle of pegs mounted on wall; *c*, shelf to support arm, with plaster trough to prevent movement; *d*, plaster wristlet.

As it is impossible to grasp a hand-grip when the extensors of the wrist are paralysed, the horizontal force could not be measured directly. Instead, the torque exerted was measured by means of a plaster-and-metal wristlet attached by a cable to the tension gauge already described. The wristlet fitted snugly over the styloid processes of radius and ulna, and showed no tendency to slip either up or down. The gauge could be slipped on to one of a circle of pegs mounted on a wall. The length of cable was adjusted so that

$$\text{cable length} = \sqrt{[(\text{radius of circle of pegs})^2 - (\text{forearm length})^2]}.$$

Thus, by Pythagoras' Theorem, the angle between cable and forearm was always 90° .

In some experiments all the flexors, except biceps and brachialis, were paralysed by injecting a small amount of 4% procaine close to the radial nerve, about 12 cm. above the elbow. The resulting paralysis was complete for about an hour, and disappeared in 2-3 hr.

From the torque and the angle of the forearm, the horizontal component of the isometric force was calculated. A correction was made for the weight of limb and wristlet, which also exert some torque on the forearm. The variation in P_0 over the experimental range of movement ($140-80^\circ$) is 13%, the tension increasing with increasing length of muscle. Most of the variation is in the first 20° of flexion, after which the isometric tension stays relatively constant.

To derive the tension-length diagram of individual muscles from measurements of the whole limb is a complicated problem. As the elbow flexes, the muscles alter in length at different rates; so at any particular position of the

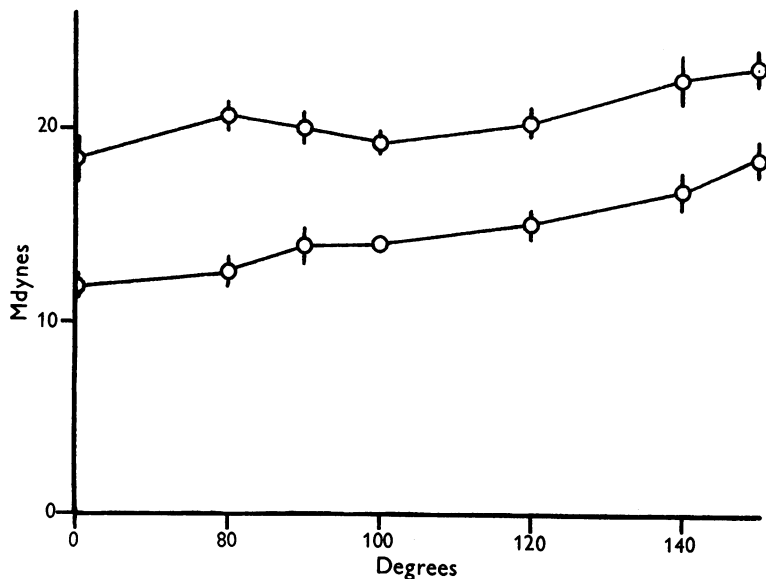


Fig. 13. Horizontal isometric tension produced at different angles of flexion. Subject M.R. Abscissa: angle between forearm and horizon. Complete extension = 180° . Ordinate: horizontal component of isometric tension, means of eight observations. Vertical bars: $6 \times$ S.E. of mean. A, all flexors together; B, biceps and brachialis only.

limb they are almost certain to be on different parts of their tension-length curve. This makes it difficult to share the total tension between them on the basis of their relative cross-sections. Arbitrary assumptions on these points have been made by previous investigators (Franke, 1920; Hansen & Lindhard, 1923; Fenn, 1938). Reduction of the number of muscles involved simplifies analysis considerably, and the method attempted utilized only two assumptions: (1) that the percentile tension-length diagram of biceps was the same as that of brachialis, that is, that they were composed of similar fibres; (2) that the shape of their tension-length curve could be represented adequately by a four-term polynomial. Unfortunately, the patterns of shortening in the two muscles of the chosen subject were so similar that the resulting set of simul-

taneous equations, which were kindly investigated by Dr E. T. Goodwin of the National Physical Laboratory, proved to be malconditioned.

Ralston, Inman, Strait & Shaffrath (1947) have constructed tension-length diagrams obtained directly from measurements on the isolated muscles of human amputees. However, their results cannot be taken to represent the properties of *normal* human muscle, for their tension-length diagram of biceps (fig. 4, p. 615) shows a maximum change in length of only 0.9 in. (2.3 cm.), starting from the point at which no tension is developed. The shortening of biceps during a normal flexion is three times as great as this (Braune & Fischer, 1890), and is certainly not attended by so great a variation in tension; moreover, the maximum tension shown in their graph is less than one-fifth of that developed by a normal muscle.

The problem of excitation

In order to interpret experiments made on the whole limb it is necessary to decide whether the excitation resulting from maximal voluntary effort is constant throughout each movement, and whether it is the same in efforts made under different circumstances. The word 'excitation' is used to describe both the number of active units, and the degree of their activity, for the mechanical response is determined by both factors.

The constancy of the mechanical response at all times makes it very likely that the excitation does remain constant, but a direct investigation has also been made by recording electromyograms during the movements.

There are two distinct aspects to the investigation:

(A) To decide whether activity in the *agonist* muscles is constant in maximal efforts, no matter how other conditions change.

(B) To decide whether there is sufficient activity in *antagonist* muscles significantly to oppose the action of the agonists. If there is, and if this opposition varies, it may prove impossible to analyse the movement at all.

The quantitative interpretation of electromyograms

The action potentials picked up from a single motor unit during activity are all the same size and shape, mono-, di- or tri-phasic depending on the position of the electrode (Dirken & Siemelink, 1941; Denslow & Hassett, 1943; discussed theoretically by Pritchard, 1930). Increase in the activity of the motor unit is brought about by an increase in the frequency of discharge, the wave-form remaining constant. The Electromyogram (e.m.g.) is the record of potential changes picked up from many such motor units, between needles or skin electrodes some distance apart. This record is quite different from that of a single motor unit, for it consists of large irregular waves whose amplitude increases with increasing activity of the muscle. In spite of the irregularity there often appears to be a fundamental frequency of about 50 cyc./sec. This

rhythm has been considered to result from the synchronous discharge of anterior horn cells, though the amplitude of the e.m.g. at any instant depends as much on the phase-relations between contributing action potentials as on their frequency. Moreover, Dirken & Siemelink (1942) have shown that the peaks of the e.m.g. waves are not related in time to the action potentials of the underlying motor units. They suggest that the e.m.g. is determined statistically from the accidental differences between action potentials in different motor units.

Whatever the underlying mechanism may be, it has been demonstrated empirically (Haas, 1926; Inman, Saunders & Abbot, 1944) that in general terms, the amplitude of the waves increases as the weight supported in an isometric contraction increases. A variety of different measures of the amplitude have been used: mean height of waves (Haas, 1926); integral under curve (Ralston *et al.* 1947), and others; the number of waves greater than a certain size (Kennedy & Travis, 1947); or other combined parameters (Dempster & Finerty, 1947). As none of the measures has a theoretical foundation, the choice between them should be made on grounds of convenience.

One limitation intrinsic to all such measurements is that, as the waves vary considerably in size, the precision of estimation of *any* collective parameter (mean height, integral, etc.) must fall off rapidly as the length of record available diminishes. This limits the value of such measurements in quick movements, where in any case, no relationship between mechanical and electrical activity has been demonstrated. Only the most general quantitative interpretation is put on the electromyograms described below.

Reciprocal innervation

The role of antagonists in voluntary movement has been hotly disputed in the past. Some authors have maintained that anatomically antagonistic muscles showed reciprocal innervation; others that both groups always contracted simultaneously.

Apart from the technical difficulty, that a passive muscle may show potential changes conducted from an active neighbour, much confusion seems to have arisen from failure to define the mechanical conditions in the movement that has been studied.

Speaking very broadly, there are two types of voluntary movement:

(1) Movements in which only small external forces are involved, for example, relatively slow movements of the unloaded limb. In such movements precision and rigidity are increased by simultaneous contraction of agonists and antagonists; for in this way the sensitivity to small deflecting forces is decreased. This view is supported by the experimental findings of Brücke (1877), Rieger (1882), Tilney & Pike (1925), on precise movements; and of Wacholder & Altenburger (1926*b*) on voluntary rigidification.

(2) Movements against opposed external forces, or quick movements in which reaction provides an opposing force, are accompanied by relaxation of antagonists. This finding has been reported by Demeney (1890), Beevor (1891), Wacholder & Altenburger (1926*a, b*) and Hoefer (1941).

The experiments of Golla & Hetwer (1924, pp. 62-63) illustrate clearly the difference to be expected in the two types of movement. In those of Hathaway (1935) the mechanical conditions are not defined, as they had no relation to the object of the research, but one record (fig. 2, p. 292) shows only slight antagonistic activity in a moderately fast extension of the unweighted forearm.

Animal experiments have increased confusion, for cortical stimulation can give rise to either type of movement, resulting in reciprocal innervation (Sherrington, 1894), or co-contraction (Tilney & Pike, 1925). This difference has been shown to depend on the strength of stimulation (Bosma & Gellhorn, 1946).

METHODS

It appeared that no electromyographic experiments had been performed under precisely the same conditions as the mechanical experiments reported above. Recordings were accordingly made from biceps and triceps during maximal voluntary flexions.

Amplifiers. Two independent capacity-coupled amplifiers connected to two pens of a Hughes four-channel recorder, recording on dry electrolytic paper. Overall frequency response maximal at 100 c.p.s., 3 db. down at 40 and 250 c.p.s.

Displacement indicator. The axle of the isotonic lever was attached to the contact arm of a sine-cosine potentiometer, arranged to provide a voltage proportional to the horizontal component of the displacement of the hand. This signal deflected the third pen of the recorder, while the fourth channel was used to register time marks every 50 msec.

Electrodes. Originally skin electrodes were used. They were made by soldering thin flex to 4 B.A. washers, the component wires being splayed out so as to cover the hole and leave a hollow for electrode jelly.

With these electrodes localization was poor: even in isometric flexions, in which triceps was palpably relaxed, potentials were picked up by conduction from biceps. By using needle electrodes localization was certainly improved, but the volume of muscle in which activity could be detected was very small.

The compromise finally adopted was to use bare hypodermic needles 2 cm. apart in triceps, retaining skin electrodes 2 cm. apart over biceps. It is essential that the electrodes should cause no discomfort, for otherwise it is quite impossible for the subject to make an unguarded maximal effort. This condition was secured by using very sharp needles inserted about 10 and 12 cm. below the origin of the muscle. In this region there is only slight movement between skin and underlying muscle, and with luck positions can be found in which the needles are quite imperceptible.

Mechanical arrangements. The isotonic lever was arranged in exactly the same way as already described, except that the weights were not held up at the end of the movement by the catch.

RESULTS

The result of a typical experiment is shown in Fig. 14. Two facts are demonstrated in these records:

(1) Action potentials appear in biceps some time before any movement is apparent, as described by Hathaway (1935). So far as one can judge from the

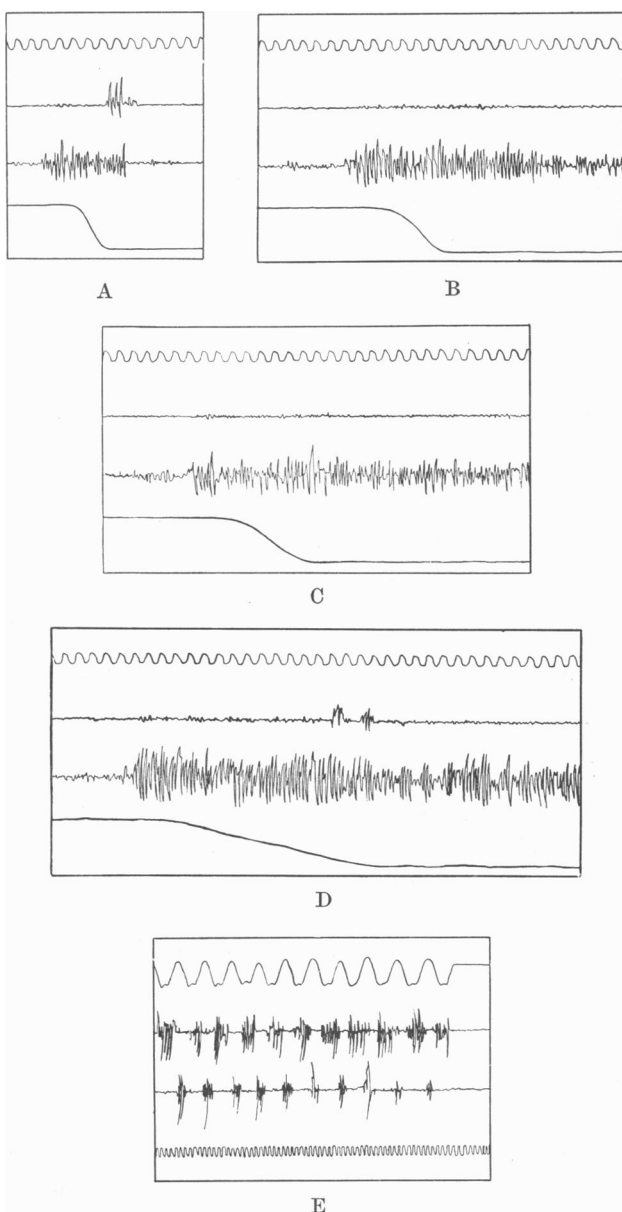


Fig. 14. Electromyograms showing reciprocal innervation. Four channels from above downwards. Time, 20 cyc./sec. Amplifier: needle electrode in triceps. Amplifier: skin electrodes over biceps. Displacement indicator: downward deflexion of trace proportional to horizontal component of hand movement during flexion. Maximal efforts. Subject J.H. A. Inertia of arm and lever only. B. Additional isotonic force of 2.47 megadynes, held up by subject at end of movement. C. Isotonic force 5.40 megadynes, held up. D. Isotonic force 7.0 megadynes, held up. E. Rapid to-and-fro movement of forearm.

amplitude of the record, activity has reached its maximum before movement begins: it also appears that the degree of activity is practically the same under different conditions of loading.

(2) Activity in the antagonist appears only in records A and D. In record A the function of triceps is clearly to check the rapid movement of the limb. This is no longer necessary when there is an opposing isotonic force. The significance of the twin outburst of activity in D is not clear. It occurs just at the end of the movement, so it may be that the limb is rigidified in preparation for the heavy load it must support.

DISCUSSION

An independent investigation of the same problem has been made recently by Dern *et al.* (1947), and I should like to take this opportunity to thank Dr R. Dern for his kindness in allowing me to see the typescript of their paper, as well as his own Ph.D. thesis on the same subject.

Most of their experiments were made in angular measure (torque, angular velocity, moment of inertia), instead of linear measure; so it is difficult to interpret them in terms of muscle function. Their general conclusion is that a constant torque is produced by the flexor muscles over a considerable part of the movement. This is not necessarily inconsistent with the theory put forward in this paper. When velocity-time curves (Fig. 5A, p. 259, 4.53, 13.42 megadynes) were transposed to circular measure, it was found that the torque exerted by the muscles did remain constant, but for only 100 and 50 msec. respectively in the two cases.

Moreover, in experiments in which Dern *et al.* applied horizontal isotonic forces, they obtained hyperbolic force-velocity curves. The high values obtained for a/P_0 (0.43–0.63) are to be expected if no correction is made for inertia.

Thus the only major difference in experimental findings is that Dern *et al.* find sufficient activity in antagonist muscles throughout movement to prevent any interpretation in terms of the function of individual muscles. This does not appear to be the case in the present experiments, nor would it be expected from the observations of other investigators (see p. 273).

Hill's equation is a very convenient one for describing force-velocity curves, and all those encountered so far have been easily fitted. No attempt is made to identify it with any particular mechanism of contraction, for, depending on the number of mathematical constants allowed, many other equations could be devised to fit as well. The adoption of any other equation would not affect the predictions made of the force-velocity and tension-time curves, since these are based strictly on the two hypotheses:

(1) That the velocity of maximal contraction depends only on the tension. (No particular mathematical function is specified.)

(2) That there is an elastic element in series with the contractile one.

Comparison of human with other muscle. In determining the relationship between force and velocity in human muscle, apart from skeletal and nervous complications, most of the difficulties have been associated with the high inertia of the forearm, which made an elaborate mechanical analysis necessary.

In work on isolated frog muscle these difficulties may be largely avoided by working at 0° C., when the speed of contraction is considerably reduced, and by arranging that the inertia of the lever, unlike that of the forearm, is 'geared down' to the muscle. In addition, the intrinsic properties of the muscle make it less sensitive to inertia. The values of P_0 and V_0 are approximately 20 kg. wt., 700 cm./sec. for a man; 50 g. wt. and 5 cm./sec. for a frog sartorius at 0° C. To have the same effect on both muscles the inertias required will be in the ratio 20/0.7:50/5, or about 3:1. That is, a sartorius lever must have an equivalent mass of 200 g. to have the same delaying effect as the forearm.

Optimal conditions for doing work. The rate of doing work is zero when $P=0$ or $P=P_0$, and maximal when

$$\frac{P}{a} = \sqrt{\left(1 + \frac{P_0}{a}\right)} - 1 \quad (\text{Hill, 1938}).$$

During the movement of flexion of the elbow the maximal rate of working attained is surprisingly high: in the case of subject M.R., for example, when $P=7$ megadynes, $V=200$ cm./sec.; the power output is then 140 W., or one-fifth of a horse-power.

Many everyday appliances are designed so as to enable a given task to be performed at the optimal rate of working. It is the necessity for matching that determines the gearing of bicycles, for example, or the size of hand implements. Detailed knowledge of muscle physiology cannot yet be substituted for practical judgement in the design of such appliances: except possibly in the case of surgical prostheses they involve movements too complex for mathematical analysis. However, the principle involved must be recognized by designers. Fast movement cannot be achieved in the presence of heavy loading: a subject can best perform a mechanical task if it is matched to the properties of his muscles.

SUMMARY

1. The relationship between isotonic force (P) and velocity of movement (V) has been studied in maximal flexions of the elbow.
2. After correction for the inertia of the forearm the $P:V$ curve can be represented by Hill's equation

$$(P+a)(V+b)=(P_0+a)b,$$

where P_0 is the isometric tension, a and b are constants. a/P_0 varied from 0.20 to 0.48 in five subjects.

3. The hypothesis that there is an inert elastic element in muscle makes it possible to relate experimental isotonic and isometric contractions to the $P:V$ curve.

4. The problem of deriving muscle properties from measurements on the whole limb is examined. The geometry of the flexor muscles and their tension-length diagram are investigated, and it is shown to be unlikely that all the muscle fibres involved have identical properties.

5. The quantitative interpretation of electromyograms is discussed. Antagonist activity is shown to be absent during experimental movements.

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APPENDIX A

A method of correcting for inertia

Owing to the limited range of movement of the elbow joint, and to its own inertia, the forearm does not have time to reach its full velocity. If it is assumed that the muscle obeys the characteristic equation the size of the velocity deficit can be estimated for a given length of pull. The method of calculation is due to Prof. A. V. Hill. On integrating equation 1 (p. 254),

$$t = -\frac{MV}{(a+F)} - \frac{Mb(P_0+a)}{(F+a)^2} \log \left(1 - \frac{V(F+a)}{b(P_0-F)} \right).$$

This equation describes how the velocity rises with time during a single contraction. The theoretical final velocity at $t = \infty$, which is the same as the velocity disregarding inertia, is $V_1 = \frac{b(P_0-F)}{F+a}$ from the characteristic equation. Inserting this above, putting

$$\alpha = \frac{P_0-F}{P_0+a},$$

and

$$\beta = \frac{(F+a)^2}{(P_0+a)Mb},$$

then

$$\beta t = -\log \left(1 - \frac{V}{V_1} \right) - \alpha \frac{V}{V_1}.$$

Differentiate with respect to t and rearrange, putting $dV/dt = dV/dx \times dx/dt$, where x is displacement,

$$\beta = \frac{dV}{dx} - \alpha \frac{V}{V_1} + \frac{V_1}{V_1 - V} - 1.$$

Integrate, putting $x=0$ at $V=0$,

$$\beta \frac{x}{V_1} = -\log \left(1 - \frac{V}{V_1} \right) - \frac{V}{V_1} - \frac{1}{2} \alpha \frac{V^2}{V_1^2}.$$

This equation describes how the velocity rises with the distance pulled. As V/V_1 is very nearly unity in practice, this equation can be simplified. Put $V/V_1 = 1 - Z$, when terms in Z and Z^2 can be neglected in comparison with $-\log Z$. Then

$$\beta x/V_1 = -(\log Z + 1 + \alpha/2),$$

which is the expression required. V_1 , α , β , and x are known from the provisional characteristic equation, the force F and the measured length of pull. Z , and from it V/V_1 , can therefore be calculated. The experimental values of velocity are then divided by V/V_1 to obtain an estimate of the theoretical final velocity.

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